



## Resistance to water deficits and recovery post-stress of native and naturalized grasses from Campos grasslands

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### Abstract

In the context of high and increasing rainfall variability in southern South America, animal production systems in subtropical *Campos* grasslands would benefit from adaptive drought management. To better understand the ability of forage species to cope with, and recover from, water stress episodes of variable intensity, a greenhouse experiment was carried out to evaluate two C3 grasses (*Bromus auleticus*, *Lolium arundinaceum*) and three C4 grasses (*Andropogon lateralis*, *Paspalum dilatatum*, *P. notatum*). To assess resistance to water deficit, plants growing in individual 12-L pots were kept for 52 days at four levels of constant water availability: 10, 30, 50 and 70% of soil field capacity (SFC). To assess the recovery capacity, pots were re-watered and maintained for 42 days at a constant 75% SFC. During the stress phase, the minimum proportion of SFC that allowed maximum forage productivity was lowest in *P. notatum* (39%), intermediate in *P. dilatatum* (50%), *B. auleticus* (61%) and *A. lateralis* (64%), and highest in *L. arundinaceum* (70%). During the recovery phase, the minimum proportion of SFC from which maximum growth was re-attained was ~30% in all species, except for *P. notatum*, which was able to fully recover even from the 10% SFC treatment. Therefore, species differed in their ability to resist drought, but less so in their capacity to recover post-stress, with the notable exception of *P. notatum*, which exhibited the lowest critical soil moisture for both resistance and recovery. Integrated with information on the potential of each species to stockpile forage, these results could inform the design of adaptive drought management strategies targeted to specific plant communities of the highly diverse *Campos* grassland, so that extensive animal production systems can be effectively buffered from recurrent, frequent, but difficult to predict in their timing and intensity, episodes of water deficits.

### Introduction

Water availability is a major factor limiting grasslands productivity in southern South America (Huxman et al. 2004; Rodríguez Palma et al. 2024). Future climate change scenarios are expected to further increase inter- and intra-annual rainfall variability (Grim 2010). Severe droughts sometimes induce large plant

mortality, thus decreasing livestock production (Breshears et al. 2016) or increasing supplementation costs (Cazzuli et al. 2024). Therefore, understanding the implications of different rainfall regimes on dominant native and naturalized species of high-diversity *Campos* grasslands is key to adaptive management strategies that help these grasslands resist and recover from drought episodes.

The response of productivity to extreme rainfall variability varies among species (Jentsch et al. 2011), ranging from minor effects to severe declines accompanied by prolonged recovery periods (Breshears et al. 2016). Such variability in grass species' drought resistance (capacity to grow under drought) and drought recovery (production after drought) (Tilman and Downing 1994) depends on grass species attributes and the magnitude, duration, and season of the drought. Since effective plant strategies under drought depend on drought-stress intensity (Lüscher et al. 2022), dominant grasses response (productive response) must be evaluated concerning this climatic driver (drought) at different available water levels.

Soil water availability is a primary factor limiting grassland productivity (Knapp et al. 2002). When soil water availability increases, an increase in forage plant growth is observed. However, this relationship between soil water availability and plant growth has a limit. Once an optimal level of soil water is reached, adding more water may not result in extra plant growth. In this context, different species have different water requirements, so some plants may be more drought-tolerant.

Estimating the impacts of droughts on high-diversity grasslands is challenging due to a limited understanding of the nonlinear responses of plant species to increasing drought conditions (Ingrisch et al. 2022), specifically the ability of dominant forage species to cope with and recover from water stress periods of varying intensity. The main hypotheses of this study are: i) water stress periods of variable intensity generate different responses in forage production in five native and naturalized grasses and ii) drought-resistant species exhibit the highest capacity for recovery following water stress periods.

## **Methods**

### ***Experiment Location***

The experiment was carried out with potted plants in a glasshouse at the INIA Tacuarembó research station, Uruguay (31°44'19.30''S, 55°58'41.48''W). The experiment began on 07/01/2021 and ended on 14/04/2021. The mean air temperature was 24°C in January and 21°C in April, similar to historical averages (24 and 18°C).

### ***Treatments, Experimental phases and Measurements***

Two C3 grasses (*Bromus auleticus* and *Lolium arundinaceum* (Schreb.) Darbysh.) and three C4 grasses (*Andropogon lateralis*, *Paspalum dilatatum*, and *Paspalum notatum*) were planted in a 12-L pot (30 cm diameter) three months before the start of the experiment. The soil substrate contained 38 ppm of Bray 1 phosphorus; 0.46 meq/100 g of potassium; 11 % organic matter, 16.6 meq/100 g of calcium and pH=5.8. Furthermore, the equivalent of 40 kg N/ha (urea) and 10 kg P/ha was applied. The soil field capacity (SFC) was calculated as 0% when the substrate was completely dry and 100% at full capacity after 48 hours of free drainage.

Plants were subjected to four constant water availability treatments (10, 30, 50, and 70 % of SFC) for 52 days, from 07/01 to 03/03/2021 (Phase I “resistance”). Then, pots were re-watered to bring them to 100% field capacity for 3 days, and then all the pots were maintained at 75% SFC for 42 days, until 14/04/2021 (Phase II “recovery”). Pots were weighed daily and watered to the required level according to the treatment. The foliage was harvested in all the pots at the beginning of the experiment, at the end of phases I, and II

by cutting plants at 2 cm. Fresh shoot mass was weighed and then dried at 60 °C for 72 hr to determine dry matter concentration.

### ***Experimental design and statistical analysis***

Treatments were arranged in a completely randomized design with four replications (pots). Analysis of variance (ANOVA) of forage production was performed for the drought phase and the recovery phase, using the Tuckey method to compare means with a 0.05 significance level.

The relationship between shoot growth and SFC percentage was modelled using nonlinear segmented regression to find threshold SFC percentages for maximal shoot growth of each species (i.e. critical SFC) and estimate the range using the SFC mean +/- two standard errors. Afterwards, to check whether the most resistant grass species has a greater capacity for recovery at different percentages of soil field capacity (SFC) a regression analyses were performed to analyse the relationship between critical SFC and recovery ability, calculated as the relative rate of shoot growth in a specific SFC treatment compared to the 70% SFC treatment. All the statistical analyses were performed with the INFOSTAT program.

## **Results**

### ***Drought resistance***

The magnitude of the reduction in grass shoot growth in response to lower water availability in Phase I was species-dependent (Fig. 1). *P. notatum* had higher biomass production than C3 grasses when water was most limiting (10% SFC). During the drought resistance phase, the modelled critical relative moisture content -the minimum percentage of SFC that allows maximum forage productivity- was lowest in *P. notatum* (39%), intermediate in *P. dilatatum* (50%), *B. auleticus* (61%) and *A. lateralis* (64%), and highest in *L. arundinaceum* (>70%).

### ***Post-drought recovery***

An interaction between species and SFC treatment was also identified for biomass production in the recovery phase (Fig. 1). Like in the previous phase (resistance), *P. notatum* had a higher biomass production than C3 grasses after the 10% SFC treatment. However, after 30% SFC treatment, *L. arundinaceum* produced more forage than both species of *Paspalum*, and *B. auleticus* produced more than *P. dilatatum*.

### ***Relationship between drought resistance and recovery phases***

*Paspalum notatum* combined greater drought resistance with better recovery from the most limiting water level (10% SFC) than any other species. In both species of *Paspalum*, forage production in the resistance phase was not related to recovery phase production. However, *L. arundinaceum*, *B. auleticus*, and *A. lateralis* showed some positive linear relationships between their growth in the resistance phase and during the recovery phase (Table 1) but only for the most extreme drought treatment (10% of SFC). Nonetheless, the water needed to reach the optimal productive level was negatively correlated with subsequent recovery only in the most limiting water level of 10% SFC (Fig. 2).

Table 1. Relationship between forage production at 10% SFC in the moisture stress phase and that grown during post-stress recovery.

<i>Festuca arundinacea</i>	Recovery = 8,22 + (0,28 x Resistance)	(R <sup>2</sup> = 0,39; P < 0,01)
<i>Bromus auleticus</i>	Recovery = 5,02 + (0,69 x Resistance)	(R <sup>2</sup> = 0,56; P < 0,01)
<i>Andropogon lateralis</i>	Recovery = 2,66 + (0,72 x Resistance)	(R <sup>2</sup> = 0,60; P < 0,01)
<i>Paspalum dilatatum</i>	No significant relationship	
<i>Paspalum notatum</i>	No significant relationship	

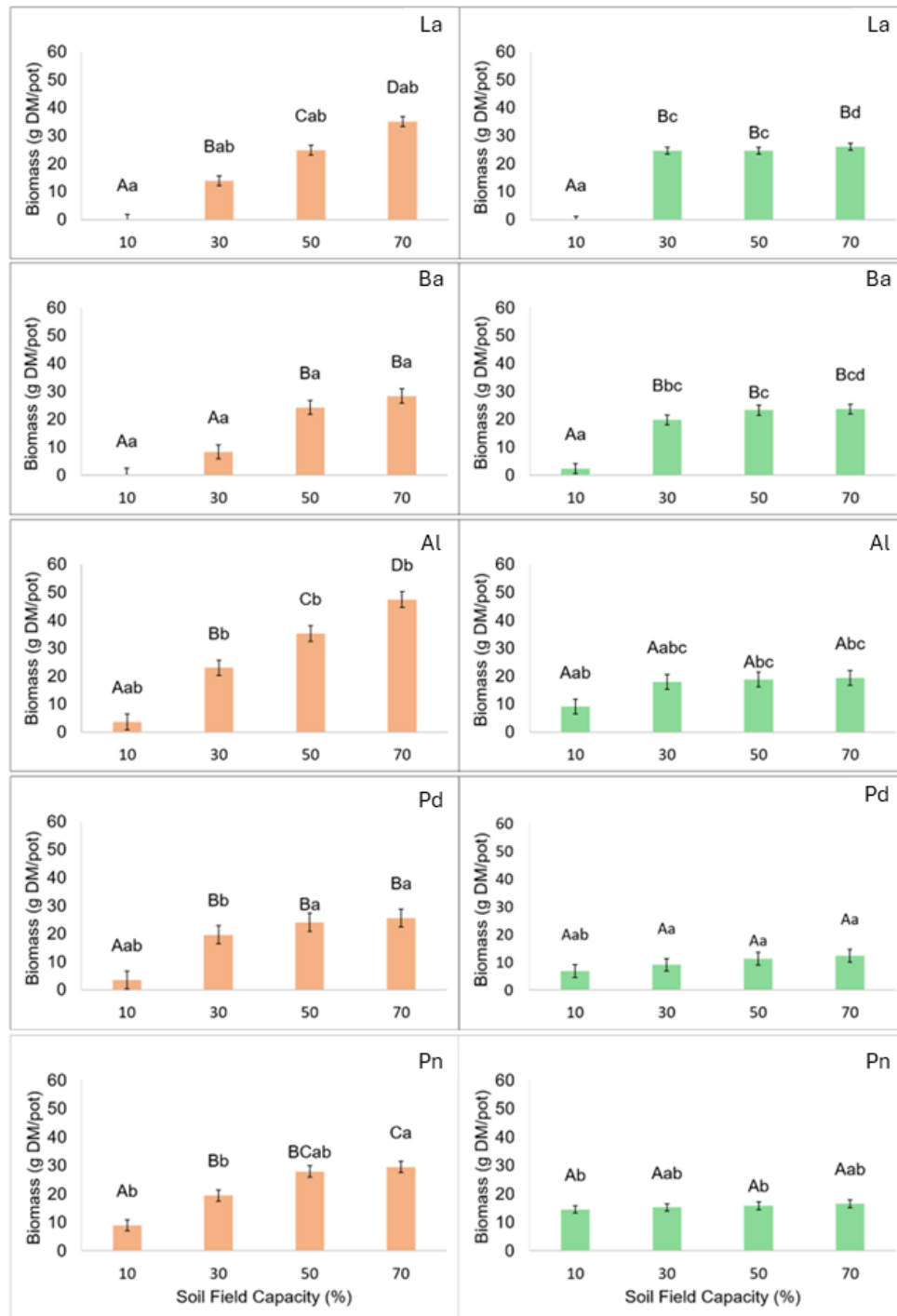


Fig. 1. Resistance (orange) and recovery (green) of forage grasses depending on the soil water content. 100%=Soil Field Capacity (water remaining in soil after 48 hours of drainage) and 0%=dried soil. La (*Lolium arundinaceum*); Ba (*Bromus auleticus*); Al (*Andropogon lateralis*); Pd (*Paspalum dilatatum*); Pn (*Paspalum notatum*). The uppercase letters indicate statistical differences between the different levels of available water (SFC), while the lowercase letters represent the statistical differences between the species assessed for the same level of water in the soil (SFC).

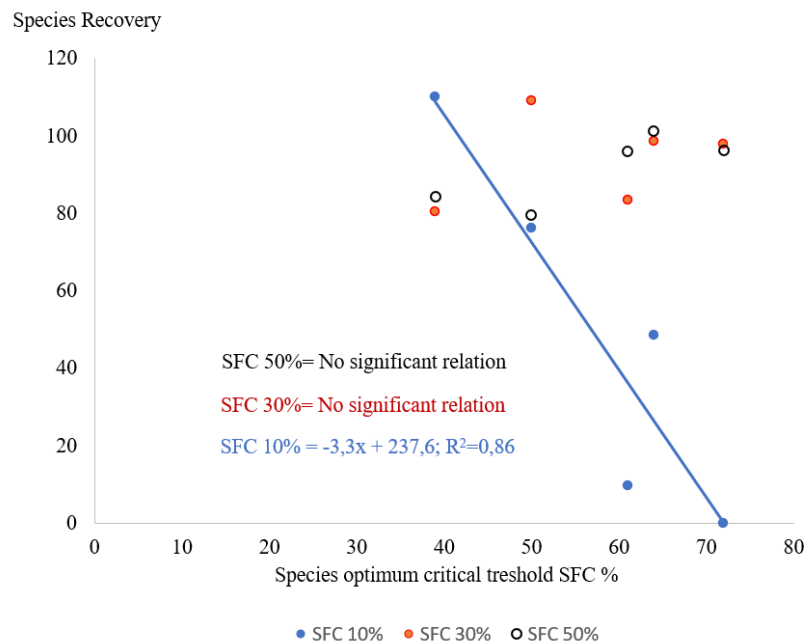


Fig. 2. Relationship between critical grass SFC water threshold and their recovery ability, calculated as the relation of species water threshold (% SFC) with their shoot production recovery in a specific SFC to the 70% SFC treatment.

## Discussion

Grass species showed different growth responses to reduced soil moisture, confirming the first hypothesis that drought resistance was species-dependent. The most drought-tolerant species were *P. notatum* (39% SFC) and *P. dilatatum* (50% SFC), while *L. arundinaceum* requires wetter conditions (>70% SFC). Therefore, our results are in line with Mackie et al. (2019) who suggested that drought resistance and recovery are more sensitive to plant community composition than to community productivity. The higher resistance of *P. notatum* to drought and its full productive recovery from low levels of water means that its management in communities where *P. notatum* is dominant is key for stability during drought disturbance. This may explain why *P. notatum* was one of the most frequent species in the *Campos* grasslands (Andrade et al. 2018). However, its advantage in subsequent recovery applies only in the most limiting water conditions, partially confirming the second hypothesis.

The negative relationship between drought recovery and forage production under severe moisture stress may be useful to improve grassland adaptive management decisions in the face of droughts. However, such responses need to be evaluated in grassland communities and integrated with information on the potential of each species to stockpile forage. Such a synthesis would provide a framework for the development of decision support systems to help design adaptive drought management strategies targeted to the specific plant communities present on individual farms in *Campos* grasslands.

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